

Responses of soil respiration to rainfall pulses in a natural grassland community on the semi-arid Loess Plateau of China

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ABSTRACT

Pulsed rainfall affects both aboveground vegetation dynamics and belowground biogeochemical processes, such as carbon cycling, in semi-arid regions. In order to study carbon released by soil respiration (SR) after rainfall pulses in natural grassland on the Loess Plateau, a rainfall simulation experiment was conducted in a grassland community dominated by a C₄ herbaceous grass [*Bothriochloa ischaemum* (L.) Keng] and a C₃ leguminous subshrub [*Lespedeza davurica* (Laxm.) Schindl] in the loess hilly-gully region. Soil respiration rate (R_s), soil temperature (T_s), and soil volumetric water content (S_v) were measured 1 day before and 1, 2, 3, 5, and 7 days after four rainfall treatments (ambient rainfall plus a 5 mm, 10 mm, 20 mm, and 30 mm rainfall pulse) and one control treatment (only ambient rainfall) in June and August 2013. Results showed that R_s and S_v largely increased one day after simulated rainfall > 5 mm. In June, the peak R_s under 10, 20, and 30 mm rainfall was $0.80\text{--}1.03 \mu\text{mol C m}^{-2} \text{s}^{-1}$ in *B. ischaemum*, with a 25–62% increase compared with the control treatment, and $0.74\text{--}1.0 \mu\text{mol C m}^{-2} \text{s}^{-1}$ (+51–104%) in *L. davurica*. In August, the peak R_s was $1.23\text{--}1.73 \mu\text{mol C m}^{-2} \text{s}^{-1}$ (+23–73%) and $1.52\text{--}1.70 \mu\text{mol C m}^{-2} \text{s}^{-1}$ (+81–102%) in *B. ischaemum* and *L. davurica*, respectively. The magnitude and duration of the increase in SR were positively related to the rainfall size, and a more considerable increase was observed in August. There was a threshold rainfall (i.e., 5–10 mm) for triggering SR increases in both months. And different responses were found between the two species, there was more substantial SR increases in *L. davurica* in comparison to *B. ischaemum*. After rainfall pulses, soil moisture and soil temperature co-regulated SR. During the relatively dry season (i.e., June), SR was negatively correlated with soil temperature and the temperature sensitivity Q_{10} value of SR was small (0.5–0.6), while it changed to positively in August and the Q_{10} was largely increased (3.2–4.3). Conversely, soil moisture was positively related to SR in both months and explained a large portion of the variation in SR (32–43% and 42–52% in *B. ischaemum* and *L. davurica*, respectively). These findings indicated that soil moisture was the major environmental factor in controlling SR in this grassland. Overall, our study suggests that SR response following rainfall pulses is species-specific within the grassland community and tends to be controlled by soil moisture, and these should be considered in the regional carbon budget assessment in the background of vegetation rehabilitation and rainfall pattern changes.

1. Introduction

Soil respiration (SR), the process of CO₂ being released through respiration by heterotrophs (e.g., soil microbes) and autotrophs (e.g., plant roots) in the soil, is a key component in the global carbon cycle and the second largest carbon efflux in terrestrial ecosystems (Schlesinger and Andrews, 2000). A small change in SR will notably

influence the atmospheric CO₂ concentration and eventually affect the climate (Schlesinger and Andrews, 2000). Spatio-temporally, SR is controlled by various biotic and abiotic factors, and among those, soil temperature and soil moisture are two principal environmental drivers (Chen et al., 2010; Davidson et al., 1998; Fóti et al., 2016; Xu et al., 2004). The dependence of SR on soil temperature is commonly found when soil moisture is not limited (Fang and Moncrieff, 2001; Lloyd and

Abbreviations: SR, soil respiration; R_s , soil respiration rate; T_s , soil temperature; S_v , soil volumetric water content; LP, Loess Plateau; Q_{10} , temperature sensitivity value of soil respiration

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Taylor, 1994). When this occurs, an increase in temperature could improve the metabolism of soil microbes and plant roots, subsequently increasing SR. On the other hand, SR could be decoupled with soil temperature and even decreased with increasing temperature under drought or extreme wet conditions; in these circumstances, soil moisture tends to be the main determinant of SR (Almagro et al., 2009; Chang et al., 2014; Wang et al., 2014; Li et al., 2008). In water-limited semi-arid regions, rainfall pulses could result in dry-wet cycles which could alter the soil micrometeorology (e.g., soil moisture and soil temperature), and consequently affect the soil CO₂ efflux, increasing its instability, and adding uncertainty for assessing the regional carbon budget.

The arid and semi-arid ecosystems dominantly determine the inter-annual variability and the changing trend of global carbon sequestration (Ahlström et al., 2015). In such water-limited areas, discrete and episodic pulsed rainfall is the major water input and it controls most aspects of ecosystem structure and function (Noy-Meir, 1973), including aboveground biological processes (e.g., plant growth) (Schwinning and Sala, 2004) and belowground biogeochemistry (e.g., carbon and nutrient cycling) (Austin et al., 2004). The increase of SR following rainfall, which is termed as “Birch effect” (Birch, 1958), has been widely reported across different ecosystems (see reviews by Borken and Matzner, 2009; Kim et al., 2012). In arid and semi-arid regions, significant and prompt increases of SR following rainfall pulses has been extensively reported in desert grasslands/shrublands (Sponseller, 2007; Cable et al., 2008; Thomey et al., 2011), semi-arid grasslands (Chen et al., 2008; López-Ballesteros et al., 2016; Wei et al., 2016), and Mediterranean forests (Almagro et al., 2009; Unger et al., 2010). Their results suggest that besides soil temperature and soil moisture, other biotic and abiotic factors also co-regulate the SR response after pulsed rainfall. Firstly, the aboveground vegetation affects the soil microenvironment and influences soil CO₂ efflux via root respiration (Raich and Tufekcioglu, 2000). Secondly, the soil properties such as soil texture, soil organic matter, and antecedent soil water content could regulate the SR fluctuation following rainfall. Cable et al. (2008) found that fine-textured soils could release more CO₂ following a pulse event, and Harrison-Kirk et al. (2013) reported that soil with more organic matter had larger SR increments, while the antecedent soil water content has been widely found to be negatively correlated with the SR responses after rainfall (Cable et al., 2008; Liu et al., 2017; Xu et al., 2004). Lastly, rainfall characteristics as could be expected, especially the magnitude and timing of pulse events greatly affect SR, and large rainfall pulses may result in more substantial SR increases than small ones, and timing could determine antecedent soil water content and other soil microenvironments (Cable et al., 2008; Schwinning and Sala, 2004; Song et al., 2012; Thomey et al., 2011).

The Loess Plateau (LP), located in the upper-middle reach of the Yellow River in northern China, is well-known for its severe soil and water erosion, sparse vegetation, and dry environment. Over the past decades, its vegetation coverage increased largely after implementation of the “Grain for Green” project which focuses on returning over-cultivated croplands to natural forest/grassland (Li et al., 2017). Currently, the natural grassland is the most widely distributed vegetation type in the region, which accounts for about 42% of the total land area of LP (Li et al., 2016). Long-term climate data suggests that annual precipitation across the whole LP region may remain unchanged, but the intra-annual variability increased with more extreme precipitation events and longer drought duration during 1961–2011 (Miao et al., 2016; Peng et al., 2017). The extensive vegetation restoration accompanied by precipitation regimes changes will undoubtedly alter the SR process in the local natural grassland. Therefore, clarifying responses of SR to pulsed rainfall in this widely distributed vegetation is significant for projecting the regional carbon budget.

Bothriochloa ischaemum (L.) (a C₄ perennial herbaceous grass) and *Lespedeza davurica* (Laxm.) Schindl. (a C₃ perennial leguminous subshrub), are the two native and dominant species in the local natural

grassland community, and both have important ecosystem functions in reducing soil and water erosion (Xu et al., 2011). Previous studies found that the two species responded significantly and positively with photosynthesis to simulated rainfall pulses, and *B. ischaemum* was more sensitive to small rainfall pulses (5–10 mm) than *L. davurica* (Niu et al., 2016; Xiong et al., 2017). These species-specific responses in carbon assimilation after rainfall may alter the community composition and structure in the long run (Niu et al., 2016). On the other hand, as the primary cause of carbon loss, the SR response to rainfall pulses remains unknown in this natural grassland community. Furthermore, plant functional traits (e.g., grass vs. legume) could influence SR (De Deyn et al., 2008), which adds uncertainty for evaluating soil carbon efflux at the community level in the background of an altered vegetation community. Thus, to investigate the effects of rainfall pulses on SR in such a semi-arid ecosystem and understanding SR response in the species-level, a simulated rainfall experiment was conducted in the two species co-dominated natural grassland community, and the SR fluctuations after rainfall were monitored. The objectives were: 1) to clarify the SR changes after rainfall events with different sizes and occurred in different growing periods, 2) to compare the response differences between the two dominant species, and 3) to distinguish the dependence of SR on soil temperature and soil moisture after pulsed rainfall.

2. Materials and methods

2.1. Site description

The study was conducted at the Ansai Research Station of Soil and Water Conservation, Chinese Academy of Sciences (109°19'23" E, 36°51'31" N), Shaanxi Province, China. The climate in the region is characterized as temperate mid-continental. The annual average temperature is 8.8 °C, with the lowest mean temperature of −6.9 °C in January and the highest mean temperature of 22.6 °C in July. Average annual rainfall is around 540 mm (1951–2000), with > 60% occurring from July to September, which is typically the rainy season. The silty loam soil was developed from wind deposits and is classified as Calcaric Cambisol (Zhang et al., 2011). The semi-arid meadow-steppe is the most distributed vegetation type and accounts for ~42% of the total land area in the region (Li et al., 2016).

The investigated grassland community is homogeneously distributed in a mountain slope (109°19'07" E, 36°51'15" N; 1150 m a.s.l.), with slope degree of 24° and slope aspect SE10°. The *B. ischaemum* and *L. davurica* are co-dominant species in the community, and other main species include *Stipa bungeana* Trin., *Artemisia sacrorum* Ledeb., *Artemisia vestita* Wall. ex Bess., and *Astragalus melilotoides* Pall. The community vegetation coverage was 57 ± 2% and 80 ± 1% in June and August 2013, respectively. The species coverage of *B. ischaemum* and *L. davurica* was 35 ± 4% and 46 ± 4% in June, 35 ± 3% and 34 ± 3% in August 2013, respectively.

2.2. Rainfall simulation

Rainfall simulation was carried out using a homemade portable rainfall simulator (Chinese patent, No. ZL2013103763306), and details can be found in Xiong et al. (2017). The sprinklers of the simulator are about 2.0 m above the grassland canopy, and the rainfall intensity was set at 0.5 mm/min, which resembles the characteristics of the local rainfall event (Zhang et al., 2017). The rainfall simulation was conducted on June 12th (relatively dry period and the beginning of the growing season) and August 15th (the rainy season and middle of the growing season) in 2013. Two study blocks were established in the homogenous grassland community, the block one was randomly chosen for the experiment in June, and the block two was for the experiment in August (see Fig. 1).

According to long-term precipitation data in 2005–2013, the local natural rainfalls were mainly small and medium events (i.e., 0–10 mm



Fig. 1. Photos of the studied grassland community taken from ‘block 1’ in June (a) and August (b) 2013, and the plot design of the two study blocks established in a homogenous grassland community. The ‘block 1’ (c) was randomly chosen for the experiment in June, and the ‘block 2’ (d) was for the experiment in August. Numbers inside of squares indicate additional rainfall amounts the plot received during the respective experimental period besides the ambient.

and 10–25 mm), infrequently accompanied by large and extreme events (i.e., 30 mm and above 50 mm) (Zhang et al., 2017). Thus, four different simulated rainfall treatments were set up as ambient rainfall plus single rainfall pulses at 5 and 10 mm (small rainfall), 20 mm (medium rainfall), and 30 mm (large rainfall), and a control treatment only receiving the ambient. Each treatment was randomly applied to a plot within one specific block, with three replicates per treatment (i.e., rainfall size; Fig. 1). The plot size was 1.0 m by 1.0 m with 1.0 m space between neighboring plots to avoid potential influences. The rainfall simulation was conducted in the early morning or late afternoon to reduce potential water loss due to evaporation.

2.3. Soil respiration measurement

The two dominant species (i.e., *B. ischaemum* and *L. davurica*) account for at least 50% of the total vegetation coverage in the studied grassland community throughout the whole growing season (Duan et al. unpublished data). Therefore, their soil respiration could well represent a large proportion of the community total and were selected for soil respiration measurement in this study. In each plot, one bunch of *B. ischaemum* and one single *L. davurica* plant were randomly selected for the measurement. All their aboveground biomass including living and dead parts were completely clipped and removed two days before the rainfall simulation to exclude the respiration from aboveground plant materials. The soil respiration rate (R_s ; $\mu\text{mol C m}^{-2} \text{s}^{-1}$) was measured between 9:00–11:00 a.m. on 1 day before and 1, 2, 3, 5, and 7 days after simulated rainfalls during each experimental period by using an enclosed-chamber CO_2 efflux measurement system (EGM-4 IRGA connected to an SRC-1 soil respiration chamber; PP-Systems, Amesbury, MA, USA). For each measurement, the CO_2 concentration was recorded for 30 s at 4 s intervals.

2.4. Environmental factors

Annual rainfall data in 2013 was obtained from a meteorological station near the study site (ca. 500 m). Soil volumetric water content (hereafter referred to as “soil water content”; S_v , %; 0–20 cm) was measured using a neutron moisture meter (CNC503B, Sper Energy, Nuclear Technology Ltd., Beijing, China) in the center of each plot. Soil temperature (T_s ; $^{\circ}\text{C}$) was measured at a 10 cm depth using digital thermometers (TP101, Xinhua Junhui Electric Appliances Factory, Jiangsu Province, China) for the soils below the studied grasses and shrubs. All measurements were performed on 1 day before and 1, 2, 3, 5, and 7 days after rainfall treatments and simultaneously with soil respiration measurements. Average air temperature (T_a ; $^{\circ}\text{C}$) between 9:00–11:00 a.m. on each day was obtained from a portable photosynthesis system (CIRAS-2; PP SYSTEMS, Haverhill, MA, USA), which was used for parallel gas exchange measurements in the same plots (Shu, 2014).

2.5. Statistical analysis

The effects of measurement month, species, and rainfall size, and their interactions on soil water content (S_v), soil temperature (T_s), and soil respiration rate (R_s) were analyzed by two-way/three-way ANOVA. The S_v , T_s , and the peak R_s values under different rainfall treatments were tested by one-way ANOVA with the Tukey post-hoc test ($P \leq 0.05$). All data were checked for normality (Shapiro-Wilk test) and homogeneity of variances (Levene's test) prior to ANOVA. The Mann-Whitney test was used to compare unpaired data in case their normality could not be obtained through data transformation. The relationship between R_s and T_s after simulated rainfall was studied using the exponential function (van't Hoff, 1898):

$$R_s = a \times e^{bT_s} \quad (1)$$

where a and b are fitted parameters. R_s and T_s are soil respiration rate and soil temperature of the two species measured on different days after rainfall. The temperature dependence of soil respiration on soil temperature is commonly expressed by Q_{10} value, which is derived by:

$$Q_{10} = \exp^{10 \times a} \quad (2)$$

where a is the parameter obtained from Eq. (1). The relationships between R_s and S_v or combining T_s and S_v were studied using the logarithmic (Eq. (3)) and binary linear functions (Eq. (4)) following Chen et al. (2008):

$$R_s = a \times \ln S_v + b \quad (3)$$

$$R_s = a \times S_v + b \times T_s + c \quad (4)$$

where a , b , and c are fitted parameters. R_s and S_v are soil respiration rate and soil water content measured on different days after rainfall treatments. All statistical tests were performed with SPSS 17.0 (SPSS Inc., Chicago, IL, USA).

3. Results

3.1. Natural rainfall in 2013

The annual rainfall was 725 mm in the study site in 2013, which was 36% higher than the long-term average (532 mm; 1951–2010). The rainfall amount during the growing season (April–October) was 709 mm, 44% higher than the long-term mean (493 mm) (Fig. 2). Before rainfall simulation in June, there were no rainfalls bigger than 5 mm, except a 13.4 mm event on April 19th, and the monthly rainfall amount in June was 66 mm. The summed rainfall amount was 590 mm during the rainy season (July–September), which accounts for 81% of the yearly total. An extremely high monthly amount (417 mm) was observed in July, which is about 3.5 times of the long-term average (118 mm). No natural rainfall events occurred three days before or seven days after the rainfall simulation during the two experimental periods.

3.2. Soil water content (S_v), air temperature (T_a), and soil temperature (T_s)

Both experimental month and rainfall treatment significantly affected S_v ($P < 0.001$; Table 1). In general, S_v in August was about 6.0%, which was 22% higher than in June (average 4.9%) across all rainfall treatments (Fig. 3). Under the control treatment, S_v remained stable (ca. 4.5%) during the experimental period in June, while in August it decreased gradually (ranged from 5.2 to 6.4%; Fig. 3). In both months, S_v under 5 mm rainfall showed similar changing trends as the control, and there was no substantial difference between values under these two ($P > 0.05$; Fig. 3). Under 10 mm, 20 mm, and 30 mm rainfall treatments, S_v increased (+16–38%) with respect to the control on the first day after rainfall and then decreased (Fig. 3). In June, S_v values under 10 mm, 20 mm, and 30 mm rainfall treatments were significantly higher than under the control and 5 mm treatments from the first to the third day after rainfalls ($P < 0.05$). On the fifth day, there were no differences among all treatments (Mann-Whitney test, $P > 0.05$). The maximum S_v value (6.1%) was observed under 30 mm treatment on the first day after rainfall, which was 38% higher than the control on the same day (Fig. 3). In August, S_v values largely increased under 10 mm, 20 mm, and 30 mm treatments (+8%, +7%, and +23%) compared with the control one day after rainfall, while there were no significant differences in S_v between rainfall treatments and the control ($P > 0.05$; Fig. 3).

Air temperature (T_a) fluctuated during the two experimental periods, and the average value was around 30 °C in both months (Fig. 4). The soil temperature (T_s) showed similar changing trends between the two species ($P > 0.05$; Fig. 4 and Table 1), but varied significantly in the two months ($P < 0.001$; Table 1). In June, compared with the control, T_s only decreased on the first day after rainfall in *B. ischaemum*,

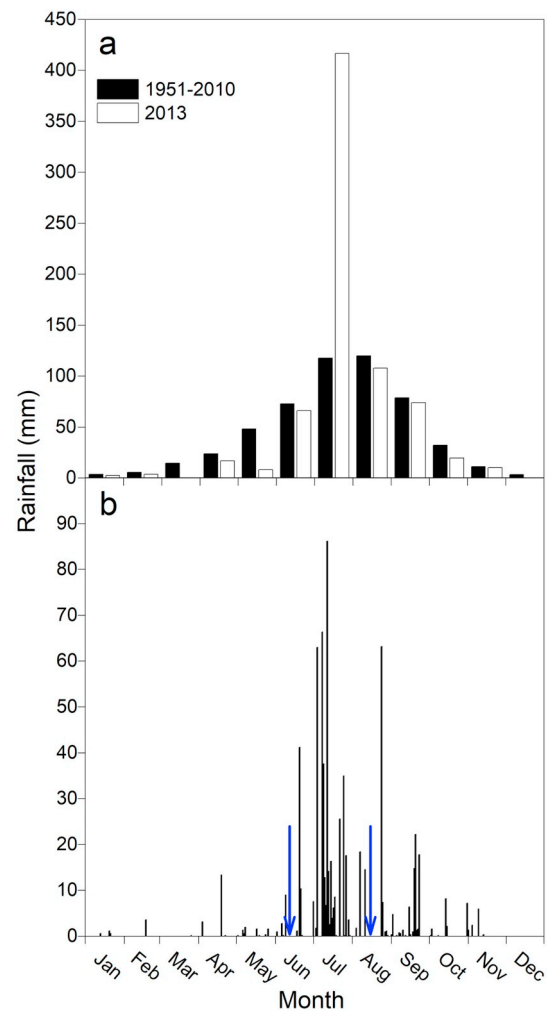


Fig. 2. Monthly rainfall in 2013 and average monthly rainfall during 1951–2010 (a) and daily rainfall data in 2013 (b). Blue arrows indicate dates for simulated rainfall experiments (June 12th and August 15th). Rainfall data were obtained from a meteorological station near the study site (ca. 500 m). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Table 1

Results of two-way/three-way ANOVA for testing the effects of the experimental month, species, rainfall treatment, and their interactions on soil respiration rate (R_s), soil temperature (T_s), and soil volumetric water content (S_v) in the investigated grassland community.

	df	R_s		T_s		S_v	
		F	P	F	P	F	P
Month	1	116.42	**	183.35	**	126.90	**
Species	1	10.57	**	0.50	n.s.	–	–
Treatment	4	20.76	**	1.52	n.s.	9.94	**
Month × species	1	0.37	n.s.	0.02	n.s.	–	–
Month × treatment	4	0.33	n.s.	0.02	n.s.	0.98	n.s.
Species × treatment	4	2.94	*	0.06	n.s.	–	–
Month × species × treatment	4	0.75	n.s.	0.40	n.s.	–	–

n.s., not significant; df, degrees of freedom.

* $P < 0.05$.

** $P < 0.001$.

and decreased by 4%, 15%, 7%, and 14% under 5 mm, 10 mm, 20 mm, and 30 mm treatments, respectively, and the values ranged from 16.9 to 18.5 °C (Fig. 4). However, in *L. davurica*, T_s decreased by a comparable extent (3–9%; ranging from 17.5 to 17.8 °C) under all (including

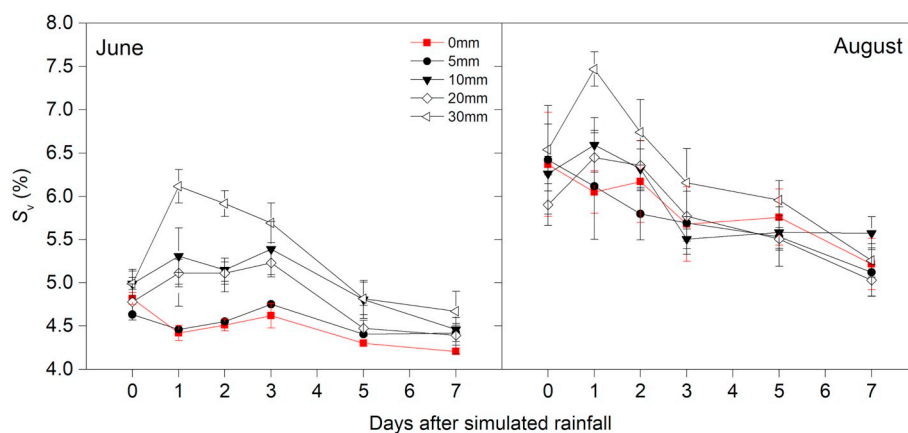


Fig. 3. Changes in soil volumetric water content (S_v) after simulated rainfall treatments in June and August 2013. Soil volumetric water content values are averages of 0–20 cm soil depth (mean \pm SE, $n = 3$).

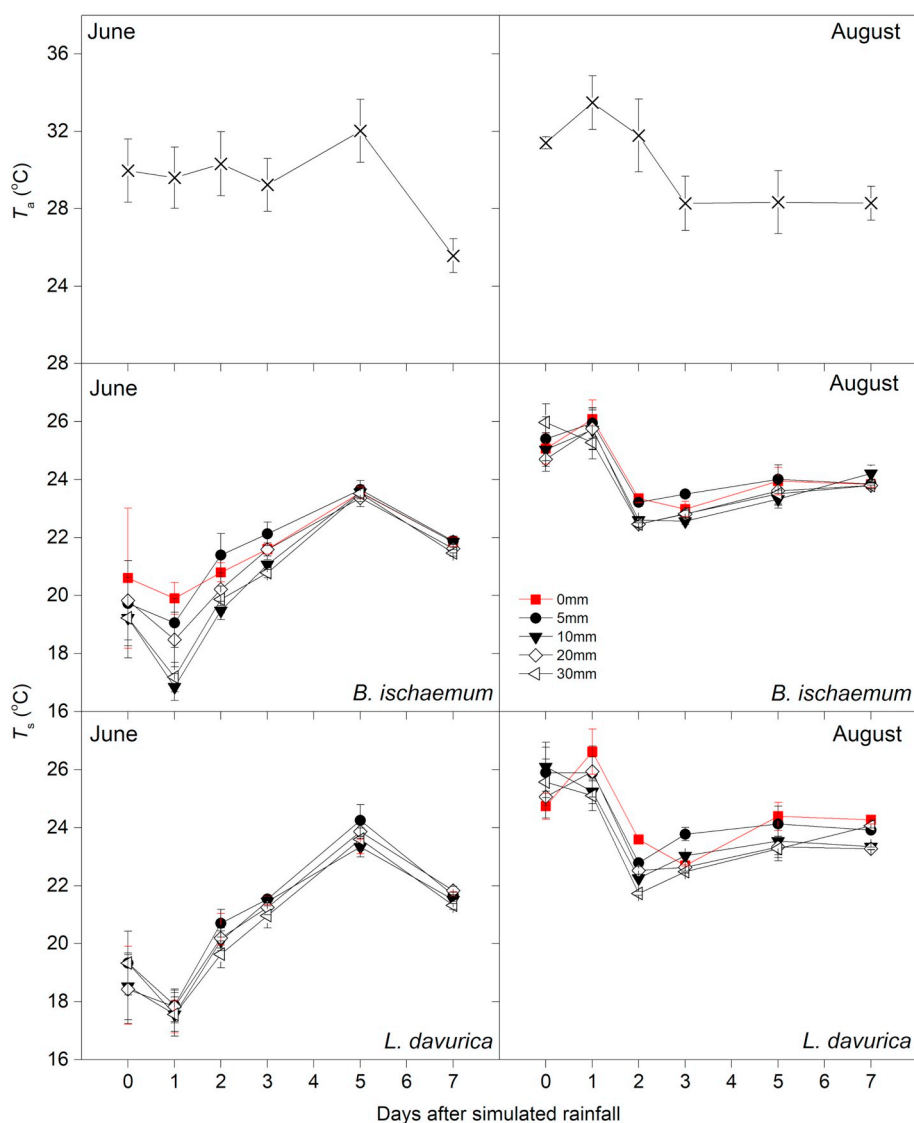


Fig. 4. Air temperature (T_a) on different days after simulated rainfall treatments in June and August 2013, and changes in soil temperature (T_s) after simulated rainfall treatments in *B. ischaemum* and *L. davurica* in June and August 2013. Both air temperature and soil temperature data are mean \pm SE ($n = 3$), and soil temperature data are averages of 0–10 cm soil layer.

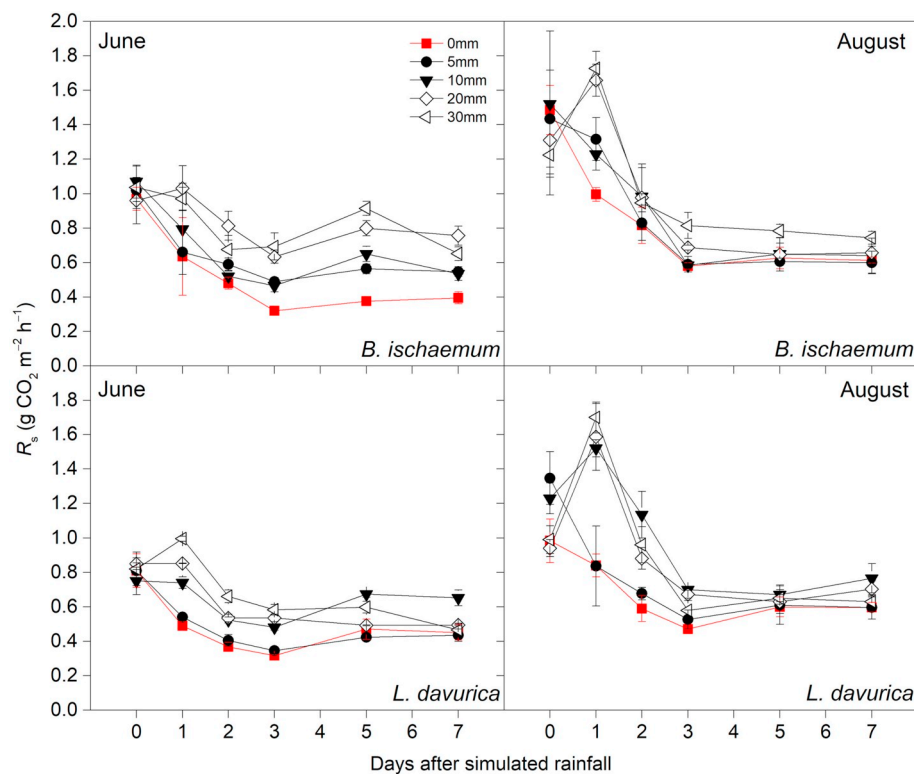


Fig. 5. Changes in soil respiration rate (R_s) of *B. ischaemum* and *L. davurica* after simulated rainfall treatments in June and August 2013. Data are instantaneous values (mean \pm SE, $n = 3$) measured between 9:00–11:00 am on each day.

control) treatments one day after rainfall simulation (Fig. 4). From the second to the seventh day, T_s increased gradually and closely followed the change of T_a in both species. In August, in comparing with the control, T_s slightly decreased on the first day after each rainfall treatment in both species, and the values were $25.7 \pm 0.2^\circ\text{C}$ and $25.8 \pm 0.3^\circ\text{C}$ for *B. ischaemum* and *L. davurica*, respectively. From the second day after simulated rainfalls, T_s started to mirror the fluctuation of T_a in both species (Fig. 4).

3.3. Soil respiration rate (R_s)

The experimental month, rainfall size, species, and interaction of species with rainfall size had significant effects on R_s (Table 1). In June, the 5 mm rainfall did not considerably affect the R_s in both species (Fig. 5). Under 10 mm, 20 mm, and 30 mm rainfall treatments, R_s largely increased compared with the control treatment on the first day, while it started to decrease and remained relatively stable towards the seventh day, and the values under rainfall treatments were higher than the control treatment until the seventh day in *B. ischaemum* and the fifth day in *L. davurica* (Fig. 5). During the whole experimental period, the peak R_s values under 10 mm, 20 mm, and 30 mm treatments were $0.80 \pm 0.27 \mu\text{mol C m}^{-2} \text{s}^{-1}$, $1.03 \pm 0.13 \mu\text{mol C m}^{-2} \text{s}^{-1}$, and $0.97 \pm 0.07 \mu\text{mol C m}^{-2} \text{s}^{-1}$ in *B. ischaemum*, which were appeared on the first day after rainfall, and were 25%, 62%, and 53% higher than the control treatment, respectively, but their differences were not significant ($P > 0.05$; Fig. 6). In *L. davurica*, the maximum values of R_s also appeared on the first day after simulated rainfalls, and were $0.74 \pm 0.03 \mu\text{mol C m}^{-2} \text{s}^{-1}$, $0.85 \pm 0.01 \mu\text{mol C m}^{-2} \text{s}^{-1}$, and $1.00 \pm 0.02 \mu\text{mol C m}^{-2} \text{s}^{-1}$ for 10 mm, 20 mm, and 30 mm treatments, respectively, which were all significantly higher than the control (+51%, +74%, and +104%) ($P < 0.05$; Fig. 6).

In August, R_s drastically increased on the first day after simulated rainfall in both species, except under 5 mm treatment in *L. davurica*, then decreased sharply since the second day and remained relatively stable

thereafter (Fig. 5). The peak R_s values occurred on the first day after simulated rainfall, and were $1.23 \pm 0.09 \mu\text{mol C m}^{-2} \text{s}^{-1}$, $1.66 \pm 0.09 \mu\text{mol C m}^{-2} \text{s}^{-1}$, and $1.73 \pm 0.10 \mu\text{mol C m}^{-2} \text{s}^{-1}$ under 10 mm, 20 mm, and 30 mm treatments in *B. ischaemum*, about 23%, 66%, and 73% higher than control, respectively. They were only significantly higher than the control under the 20 mm and 30 mm rainfall treatments ($P < 0.05$; Fig. 6). Likewise, the peak R_s values in *L. davurica* were also observed on the first day after simulated rainfalls, which were $1.52 \pm 0.05 \mu\text{mol C m}^{-2} \text{s}^{-1}$, $1.59 \pm 0.19 \mu\text{mol C m}^{-2} \text{s}^{-1}$, and $1.70 \pm 0.09 \mu\text{mol C m}^{-2} \text{s}^{-1}$ under 10 mm, 20 mm, and 30 mm treatments, about 81%, 89%, and 102% higher than control, respectively (Fig. 6).

3.4. Relationships of R_s with T_s and S_v

In June, R_s was negatively correlated with T_s in both *B. ischaemum* and *L. davurica* and could explain 10% and 25% of the variation of R_s , respectively (Figs. 7 and 8). While in August, R_s was positively correlated with T_s and explained 24% and 22% of the variation, respectively (Figs. 7 and 8). The Q_{10} values were 0.61 and 0.45 for *B. ischaemum* and *L. davurica* in June and increased to 3.22 for *B. ischaemum* and 4.31 for *L. davurica* in August, respectively (Table 2). The R_s was positively correlated with S_v in both species and months (Figs. 7 and 8), and S_v could explain 32–52% of the variation in soil respiration with the logarithmic functions. Using the binary linear function, T_s and S_v together could explain 33% and 47% of the variation in soil respiration in *B. ischaemum* and *L. davurica* in June, and 56% and 60% of the variation in August, respectively (Table 2).

4. Discussion

A significant increase in S_v and R_s was observed on the first day after rainfall pulses, then gradually decreased and had no significant difference with the control treatment on the 5th–7th day after rainfall in both species during the two experimental months (Figs. 3 and 5). Drastic but

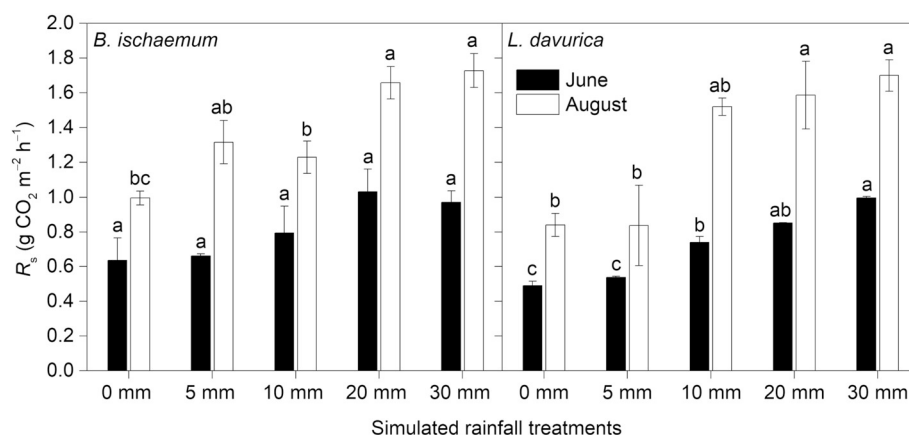


Fig. 6. The peak values of soil respiration rate (R_s) of *B. ischaemum* and *L. davurica* after simulated rainfall treatments in June and August 2013. Data are mean \pm SE ($n = 3$). Different letters above the error bars indicate significant difference among treatments in the respective month (one-way ANOVA, $P < 0.05$).

different degrees of increase in soil CO_2 efflux following rainfall/watering has been well documented in many water-limited ecosystems, e.g., in Inner Mongolian Steppe (Chen et al., 2008; Li et al., 2018), semi-arid grasslands in North America and Mediterranean regions (López-Ballesteros et al., 2016; Thomey et al., 2011), and also grassland on the Loess Plateau region (Jia et al., 2014). In this study, the burst of SR was recorded on the first day after rainfall pulses, which is consistent with the ‘Birch effect’ (Birch, 1958) and results from other above-mentioned semi-arid grasslands (e.g., Chen et al., 2008; López-Ballesteros et al., 2016). While the degree of increase was lower in this study (up to 73% and 102% in *B. ischaemum* and *L. davurica*, respectively) comparing with others, such as an 8-times increase in Inner Mongolian Steppe (Chen et al., 2008). The difference is likely due to the fact that other studies applied much larger rainfall pulses than this study (e.g., 100 mm vs. maximum 30 mm), the larger rainfall could generally trigger more

significant ecosystem responses (Schwinning and Sala, 2004). A study in grassland in SE Spain also observed an up to 8–10 times increase immediately after receiving a rainfall pulse close to our study (i.e., 15 mm), but it decreased to 2–3 times one day after watering (López-Ballesteros et al., 2016), which is similar to what we observed and this could also indicate the effect of rainfall pulses declines over time. Increased soil respiration following pulsed rainfall observed in this and other studies could be broadly attributed to mechanisms like enhanced soil microbial metabolism by more substrate supply through decomposition of dead microorganisms/fine roots/mycorrhiza and mineralization of physical protected soil organic matter caused by changes of soil aggregate in dry-wet processes, and physical processes like water displacing CO_2 accumulated in soil pores by infiltration (Borken and Matzner, 2009; Chen et al., 2008; Kim et al., 2012; Unger et al., 2010).

The size and timing of rainfall pulses control the magnitude and

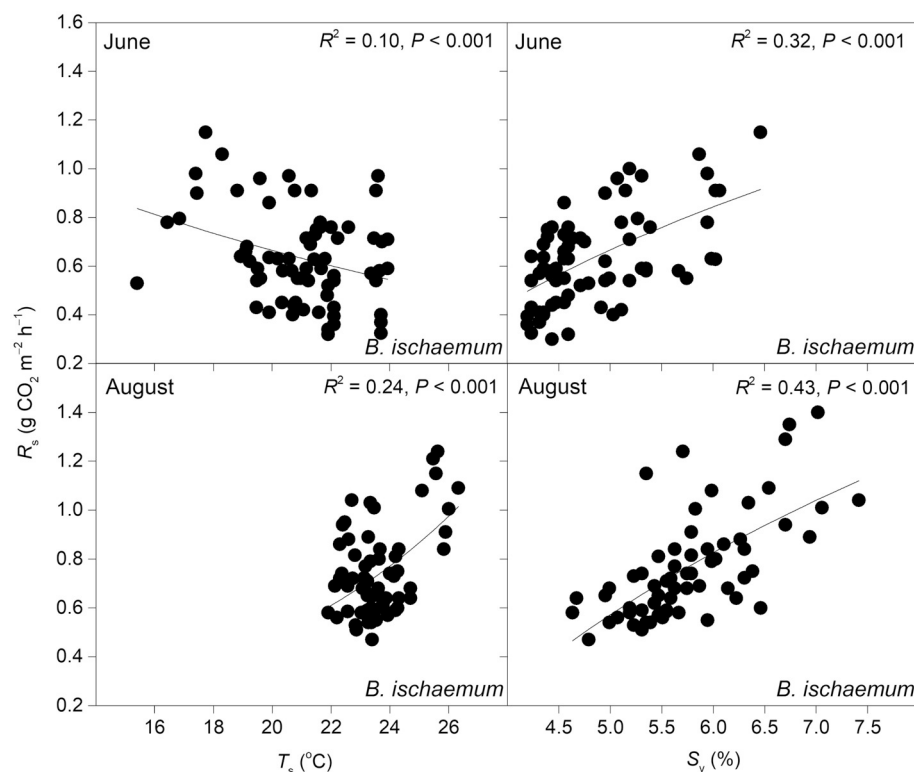


Fig. 7. Correlations of soil respiration rate (R_s) and soil temperature (T_s) and volumetric soil water content (S_v) of *B. ischaemum* in June and August 2013. The exponential function was used for fitting R_s and T_s ($R_s = a \times e^{bT_s}$); the logarithmic function for R_s and S_v ($R_s = a \times \ln S_v + b$).

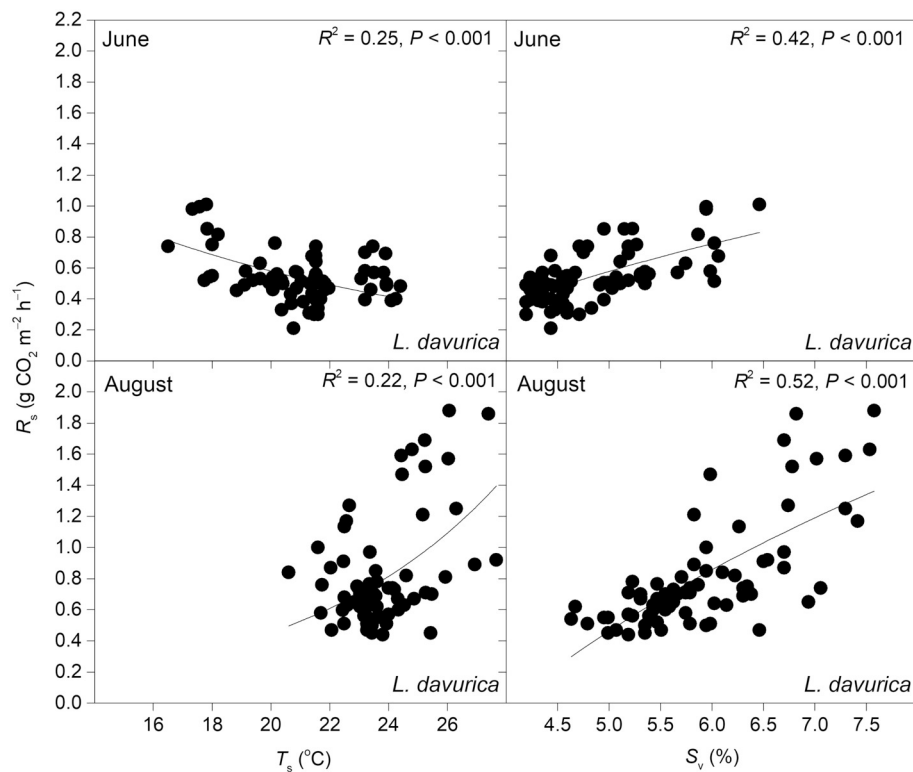


Fig. 8. Correlations of soil respiration rate (R_s) and soil temperature (T_s) and volumetric soil water content (S_v) of *L. davurica* in June and August 2013. The exponential function was used for fitting R_s and T_s ($R_s = a \times e^{bT_s}$); the logarithmic function for R_s and S_v ($R_s = a \times \ln S_v + b$).

duration of SR response in many semi-arid grassland communities (Chen et al., 2008; Song et al., 2012; Wei et al., 2016). The hierarchical response to rainfall pulses is commonly recognized in semi-arid ecosystems, which means that small pulses produce minor ecological feedbacks, and greater ones trigger substantial effects (Schwinning and Sala, 2004). These have been confirmed in this study, which clearly showed that rainfall size and month significantly affected the SR (Table 1), and larger rainfall pulses caused greater SR increase (Figs. 5

and 6). In both species and experimental periods, the 5 mm rainfall event did not have a pronounced effect on SR, while significant increases were observed in treatments ≥ 10 mm, suggesting that there might be a threshold rainfall between 5 and 10 mm for triggering SR responses (Figs. 5 and 6). Considering the aboveground biomass and litter were removed before the experiment, which excluded canopy and litter interceptions, the threshold rainfall should be larger in the natural condition. A threshold rainfall generally exists for promoting the

Table 2

Regression results of soil respiration rate (R_s) with soil temperature (T_s) and soil volumetric water content (S_v) in *B. ischaemum* and *L. davurica* in June and August 2013.

	a	b	c	Q_{10}	R^2	P
<i>R_s</i> vs. <i>T_s</i>						
June						
<i>B. ischaemum</i>	1.81 (0.64)	−0.05 (0.02)		0.61	0.10	< 0.001
<i>L. davurica</i>	3.09 (0.97)	−0.08 (0.02)		0.45	0.25	< 0.001
August						
<i>B. ischaemum</i>	0.05 (0.03)	0.12 (0.02)		3.22	0.24	< 0.001
<i>L. davurica</i>	0.02 (0.02)	0.15 (0.03)		4.31	0.22	< 0.001
<i>R_s</i> vs. <i>S_v</i>						
June						
<i>B. ischaemum</i>	0.97 (0.17)	−0.89 (0.27)			0.32	< 0.001
<i>L. davurica</i>	0.98 (0.13)	−1.00 (0.21)			0.42	< 0.001
August						
<i>B. ischaemum</i>	1.39 (0.20)	−1.67 (0.35)			0.43	< 0.001
<i>L. davurica</i>	2.16 (0.25)	−3.02 (0.43)			0.52	< 0.001
<i>R_s</i> vs. <i>T_s</i> & <i>S_v</i>						
June						
<i>B. ischaemum</i>	0.17 (0.04)	−0.01 (0.01)	0.14 (0.36)		0.33	< 0.001
<i>L. davurica</i>	0.16 (0.03)	−0.02 (0.01)	0.19 (0.26)		0.47	< 0.001
August						
<i>B. ischaemum</i>	0.23 (0.03)	0.07 (0.02)	−2.25 (0.43)		0.56	< 0.001
<i>L. davurica</i>	0.33 (0.04)	0.07 (0.02)	−2.76 (0.48)		0.60	< 0.001

R_s vs. *T_s*, the exponential function $R_s = a \times e^{b \times T_s}$. Temperature sensitivity: $Q_{10} = e^{10b}$. *R_s* vs. *S_v*, the logarithmic function $R_s = a \times \ln(S_v) + b$; *R_s* vs. *T_s* & *S_v*, the binary linear function $R_s = a \times S_v + b \times T_s + c$. Standard errors of coefficients are given in parentheses.

biological response in water-limited ecosystems, which is referred to as ecologically effective rainfall (Schwinning and Sala, 2004). Chen et al. (2008) found that only rainfall events larger than 10 mm could significantly increase the SR in the semi-arid grasslands in Inner Mongolia, which is similar to the threshold value observed in this study. While a smaller threshold (3–5 mm) was reported for the same vegetation type also in Inner Mongolia (Hao et al., 2012), this difference could probably be due to their site-specific conditions, such as drier (320–400 mm annual rainfall) than this studied site (540 mm).

After comparing the effects of rainfall events in different months, it is suggested that an R_s increase under the same rainfall pulse was relatively larger in August, particularly in *L. davurica* (Fig. 5). Previous studies indicated that rainfall pulses during the dry season with lower antecedent soil water content had greater effects on SR than that during the wet season (Cable et al., 2008; Liu et al., 2017; Morillas et al., 2017). However, this was not the case in our study, where we speculated that the wetter season in this study was still within a relatively dry range, and with larger root respiration and possibly more active microbes (Salazar et al., 2018), the increase in the wet season could exceed that in the dry season. Soil properties (e.g., soil texture and organic matter content) could also affect SR responses after rainfall. In our study, soil texture was unlikely different under the two species since they are growing in the same community. Research showed that soil with more organic matter could release more CO_2 in dry-wet cycles (Harrison-Kirk et al., 2013). The N-fixing *L. davurica* could potentially have higher soil C and N storage below it, like other N-fixing legumes in semi-arid grasslands in the same region (Wu et al., 2017). This organic matter could become available for soil microbes after watering and also the symbiotic nitrogen-fixing bacteria (i.e., rhizobia) activities could be improved after rewetting (Zahran, 1999), with all these subsequently leading to higher SR increments.

Soil temperature and soil moisture are two key factors that control SR, and the dependence of SR on these could be altered under different environmental conditions (Almagro et al., 2009). The negative relationship or decoupling between SR and T_s has been reported when the soil water content is below a certain value (Chang et al., 2014). This is also observed in this study in June for both species (Figs. 7 and 8), and it may be due to inhibited soil microbial activity and autotroph respiration under dry conditions (Almagro et al., 2009). The negative relationship between SR and T_s in the dry season could also be expressed by the temperature sensitivity Q_{10} value. Much smaller Q_{10} values were observed in the dry season (0.61 and 0.45 for *B. ischaemum* and *L. davurica* in June, respectively) compared with the wet season (3.22 and 4.31 for *B. ischaemum* and *L. davurica* in August, respectively) (Table 2), which not only indicated that SR was decoupled with T_s in the dry season, but also showed that the temperature dependence recovered in wet conditions. The SR is dominantly determined by S_v when soil moisture is below/above a certain threshold (Almagro et al., 2009; Arredondo et al., 2018; Chang et al., 2014; Xu et al., 2004). After rainfall pulses, S_v solely explained up to 42% and 52% variations of SR in dry and wet seasons, respectively, while T_s only explained up to 25% variability in either period (Table 2). By combining these two factors, the function was only slightly improved (R-square up to 0.47 and 0.60 in dry and wet seasons, respectively) (Table 2). These indicated that rather than T_s , S_v is the leading factor determining SR response after rainfall pulses in this grassland community, which is consistent with results from other types of grassland in semi-arid regions (e.g., Chen et al., 2008; Arredondo et al., 2018). A meta-analysis study also suggested that SR responses following precipitation were mainly driven by soil moisture changes rather than soil temperature across different biomes (Liu et al., 2016).

In June, the peak R_s in *B. ischaemum* under all rainfall treatments showed no difference compared to the control treatment, while in *L. davurica* the peak R_s of rainfall treatments were all significantly higher than the control except the 5 mm one (Fig. 6). The R_s increase on the first day after rainfall was also larger in leguminous *L. davurica* in

comparison to *B. ischaemum* under all rainfall treatments (Fig. 5). These suggested that the leguminous *L. davurica* responded more substantially to rainfall pulses compared to the herbaceous *B. ischaemum*. Different extents of increase in seasonal soil respiration were also reported from grassland communities with different dominated species on the Loess Plateau, and they argued that the species composition may regulate the dependence of soil respiration on soil temperature and soil moisture and thereby control SR responses after rainfall (Jia et al., 2014). But in this study, we observed similar patterns in the dependence of soil respiration on soil temperature and soil moisture between the two species. Hence, the species-specific response patterns should be likely due to the possible difference in soil organic matter which may be caused by N-fixation in *L. davurica*. Additionally, potential differences in soil microbial community between the two species could also play a role since a recent study has confirmed that legume and grass species could differentially affect soil chemical properties and the soil microbial community (Zhou et al., 2017).

5. Conclusions

Soil respiration promptly and significantly increased after pulsed rainfall in a natural grassland community dominated by *B. ischaemum* and *L. davurica* in the hilly-gully region of the Loess Plateau. The magnitude and duration of the increase were positively related to the rainfall size, and rainfall pulses in the relatively wet season produced more pronounced effects than those in the dry season. Such differences may attribute to variations in plant growth, antecedent soil water content, and other biotic and abiotic factors. A threshold rainfall between 5 and 10 mm may exist for triggering a soil respiration increase. Soil temperature was negatively correlated with soil respiration in the dry season yet switched to a positive correlation in the wet season, and soil moisture tended to be the dominant controlling factor of soil respiration following rainfall pulses. Plant functional type co-regulated the soil respiration, and N-fixing *L. davurica* could release more carbon than *B. ischaemum* after rainfall pulses. We suggest that the species-specific response patterns observed in this study should be considered in evaluating large-scale soil respiration in the background of vegetation restoration along with rainfall pattern changes in semi-arid regions.

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Declarations of interest

None.

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